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MEMOIRS
OF THE
AMERICAN ACADEMY.

I.

On the Embryology of Echinoderms.

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Communicated February 2d, 1864.

THE following account of the embryology of a few of our Echinoderms, though by no means complete, will fill several of the gaps hitherto existing in the knowledge of the development of Echinoderms; and in the hope that something may be added to our understanding of the general plan of development of Echinoderms, it is here given in its present condition, in order to show how far the plan of development is identical in the different orders of Echinoderms. I shall take up in turn the Echinoids, Ophiurans, and Holothurians, and then compare these different larvæ with what we know already of the development of our common Starfish, to see how close the agreement of the mode of formation of the young Echinoderm is in these four orders, and to satisfy ourselves how true are the suggestions made at that time, on a very superficial acquaintance with any other Echinoderm larva except that of Asteracanthion, concerning the function of many of the organs of these wonderful larvæ.

TOXOPNEUSTES DROBACHIENSIS Ag.

The larvæ of our common Echinus resemble most closely, in some of their earlier stages, those of *Toxopneustes lividus* Ag., figured by Müller on Plates VI. and VII. of his fourth Memoir.* The figures which Müller gives correspond with what I have

* MÜLLER, J. Ueber die Larven und die Metamorphose der Echinodermen. Vierte Abhandlung. Berlin, 1852.

observed in larvæ obtained by artificial fecundation. He succeeded in tracing them for about three weeks, which is not quite as long as I have kept them alive. Müller has unfortunately not given us any figures of the very first stages of this species, nor has he found the adult larvæ swimming about immediately before the absorption of the Pluteus. The series of figures found in this paper will give us a more complete idea of the different phases of growth of one species of Echinus, than can be gathered from a comparison even of the different species which Müller has investigated. It will enable us to trace the order of appearance of the arms of the Pluteus, and the last changes which the larva undergoes immediately before the young Sea-urchin has resorbed the whole framework of the Pluteus.

The process of segmentation of the yolk is entirely similar to what we observe in the Starfish; the main differences in the eggs are simply of proportion between the relative size of the yolk-mass and the outer envelope. My observations agree with the account of the segmentation given by Derbès.* The formation of the "Richtung's Bläschen" is very easily followed in the Sea-urchin.

The yolk contracts somewhat immediately after the fecundation takes place, and we might repeat here, word for word, the description of the changes which the yolk undergoes in the Starfishes, and have the history of the changes during the segmentation of the yolk of an Echinus. For an account of this I would refer the reader to the fifth volume of the Contributions to the Natural History of the United States, by Professor Agassiz. The embryo, on escaping from the egg, resembles a Starfish embryo, and it would greatly puzzle any one to perceive any difference between them. The formation of the stomach, of the œsophagus, the intestine, and the water-tubes takes place in exactly the same manner as in the Starfish, the time only at which these different organs are differentiated not being the same. We have thus very early in the history of these two orders differences which to a practised eye tell at once to which of them the young larva belongs. What is a particularly important difference is the formation in Ophiurans and in Echinoids of calcareous rods at an early period of the larval condition.

The embryo after its escape from the egg.

In the spherical embryo soon after its escape from the egg we perceive a thickening of the walls at one of the poles; a depression is then formed at this extremity, which becomes more and more marked; † the wall then turns in, and a small cavity

* DERBÈS. Ann. d. Scien. Nat. 3^e Ser. VIII. p. 80. 1847.

† See figs. 4 and 5 of my paper on Asteracanthion in Proc. Am. Acad., Vol. VI., April 14, 1863, which represent the corresponding stages of the embryo of the Starfish.

is formed, which goes on increasing in length until we have a hollow cylinder (*d*) extending half the length of the larva, as in figs. 1 and 2, which correspond to fig. 6 of my paper referred to above. In the profile, fig. 1, we notice the same tendency in the digestive cavity (*d*) to incline towards the lower side, after the dorsal portion has increased more rapidly, giving the anal part of the larva a bevelled appearance. In a somewhat older stage, fig. 3, the digestive cavity is still longer, and almost touches the lower side. We notice a difference between the Starfish and the Sea-urchin in the time of formation of the alimentary canal, the stomach, and the œsophagus. In the Starfish the mouth is formed before the differentiation of these organs takes place; while in the Sea-urchin the mouth is not formed until the alimentary canal and the œsophagus, as well as the water-tubes, are quite distinctly defined. (See fig. 8.) What is also peculiar to Echini is the presence of large masses of yolk-cells along the sides of the digestive cavity, indicative of the great changes which take place at the points where these masses of yolk-cells are most numerous. We have observed that the yolk-cells are always present wherever any new organ is developed; in these larvæ the appearance of the water-tubes is preceded by an accumulation of yolk-masses at the extremity of the digestive cavity (see fig. 3); and the place of the limestone rods, fig. 4, *r'*, is first seen filled by clusters of these yolk-masses, in the midst of which the rods are deposited. Rods extending into the arms are characteristic of Echinoids and Ophiurans; we find nothing of the kind in Starfish or Holothurian larvæ.

In the next stage, fig. 4, the original cylindrical digestive cavity has already a decided tendency to differentiation, the walls of the stomach (*d*) and of the œsophagus (*o*) being of very different thickness; from *o*, the pouches which are to become the water-tubes (*w w'*) project far beyond the outline of the digestive cavity. The limestone rods (*r' r'*) can faintly be distinguished from the mass of yolk-cells which surround them. The calcareous cells which take such a great prominence in older larvæ (see fig. 19) make their appearance as early as the stage of fig. 3; they are quite large in the condition represented in fig. 4. The strong contrast which already exists between the different parts of the digestive cavity is still more apparent in a stage but slightly more advanced, fig. 5. The dorsal portion of the larva has up to this time been growing most rapidly, changing the outline of the larva, particularly when seen in profile; in the subsequent figures, the outline, when seen from above, is also undergoing great changes. The larva assumes a more rectangular shape (fig. 6) when seen either from above or from below. The water-tubes are almost separated from the digestive cavity, which has been divided into three very distinct regions (*c, d, o*, fig. 8), the limestone rods, simply T-shaped before, fig. 5, are sending off small processes, and the chords

of vibratile cilia (v, v'), which were a simple button (v , fig. 5), are quite stout, projecting beyond the general outline when seen from above or below (fig. 6, v). It is at this advanced condition only that the œsophagus touches the lower surface, previous to the formation of the mouth, which takes place only when the larva has reached the condition of fig. 9. A view of fig. 6 seen from the anal extremity, fig. 7, shows how far it has lost its cylindrical shape and become wedge-shaped. In fig. 8, which is the same larva seen in profile, the indentation which indicates the position of the mouth (m) has changed somewhat the even outline of the lower surface; there is a marked bending of the alimentary canal, bringing the anal opening (a) still nearer the lower surface. In fact, since the first formation of an opening in fig. 1 (am), which is at once strictly mouth and anus, there is a continued tendency to bend the anal part of the digestive cavity towards the oral surface, even while this single opening performs the functions of mouth and anus, during the period which precedes the formation of the mouth, after the alimentary canal, the true stomach, and the œsophagus have been differentiated. This is somewhat different from what we notice in the Starfish embryo, where the mouth is formed before the anus has been much bent from its original position.*

The large accumulations of yolk-masses round the rods $r' r'$ cannot fail to be noticed in the stages just described, figs. 6, 7, 8. This contrasts strikingly with the Starfish larvæ, in which we find nothing of the kind; the body of the young embryo is quite remarkable for its great transparency, which only increases with age, while in the Echinus larvæ the great accumulations of yolk-masses renders them somewhat opaque even in their early stages, and the increase of calcareous cells in somewhat more advanced forms, as figs. 17, 19, makes it more difficult than in the Starfish to trace accurately the minute changes which the rods and water-tubes undergo. We now come to conditions, figs. 9 and 10, which are sufficiently advanced to enable us by comparing them with still older forms, such as figs. 16, 17, 19, to form a correct idea of the mode of transformation from the shape of figs. 9, 10, to the complicated larva represented in fig. 20. I merely refer to this comparison in a general way, as in the explanation of the different stages it will be carried out more fully, to call attention to the periods which first give us a clew to the development of the different parts, by showing us plainly which portions of the embryo must assume a great prominence, and obtain a more rapid development than others, to pass gradually through the stages which are hereafter figured. In fig. 9 the difference in the rapidity of the development

* See fig. 8, Proc. Am. Acad., Vol. VI., quoted above.

of the two water-tubes w, w' , is quite striking. The left water-tube (w') — left when seen from the aboral side, the anal extremity being turned down as in these figures — is fast pushing through the mass of the larva, and finds its way to the surface at about the condition represented in fig. 15, where the water-pore, the madreporic body, allows the water to enter freely into this water-tube. In a somewhat more advanced larva, seen obliquely from the oral side, fig. 10, we can trace the mode of development of the chord of vibratile cilia; it is formed of a single continuous line, extending round the mouth; it forms but a single shield, and not two as in the Starfish, where the first trace of this chord is the appearance of two separate arcs forming eventually two distinct plastrons. The little larva looks in this condition like a quadrangular pyramid with a rounded apex and rounded angles at the base. The corners of the base e', e'' are the origin of the first arms of the larvæ (figs. 9, 10). Owing to the great increase of the dorsal and oral parts of the larvæ, they change their general appearance very rapidly. (See figs. 11, 12.) As the intestine becomes more distinct from the stomach, the angle which their axes make grows more acute (fig. 11 c, d); the mouth (m) is removed further from the anus. The walls of the œsophagus (o) are now capable of considerable expansion and contraction; they are much thinner than those of the intestine or stomach. Fig. 12, which is fig. 11 seen from the oral side, shows the course of the vibratile chord, the position of the arms e', e'' , the great size of the rods (r'), with their branches, and the difference of level between the opening of the mouth and anus. From an examination of figs. 11 and 12 the position of the rods can be determined, one main part extending from the anal extremity to the arms e' , another extending in a curved line (fig. 11) from e' to e'' , and sending off a small branch which runs between the anus and the digestive cavity (fig. 12). This will, perhaps, be more clear on examining the larva in such a way (fig. 13) as to bring the vibratile chord into the field; this stage does not differ materially from that represented in fig. 10, the changes which have taken place defining the arms more sharply by the indentations of the vibratile chord. The intestine, the stomach, and the œsophagus are clearly distinguished by the different character of their walls. The water-tubes are not united, and have not increased in size. This condition presents a material difference in the degree of development when compared with the corresponding stage of a Starfish (fig. 11, Proc. Am. Acad.). Here the water-tubes occupy the most important portion of the larva, while in the Sea-urchin larva the most striking characteristic is the amount of room taken up by the stomach and œsophagus compared with that occupied by the water-tubes.

In the subsequent stages (figs. 14 and 15), the Echinus larvæ have reached forms

which are already more familiar to us from the drawings of Müller; they resemble closely some of the figures given by him of *Toxopneustes lividus* in his fourth Memoir. A good deal of allowance must be made for the differences of outline between the figures given here and the drawings of Müller. From the evidence of the drawings themselves, it is plain that nearly all the specimens drawn by him are compressed. I have endeavored to represent these larvæ as they appear swimming about; it is by no means an easy task to follow them in their almost unceasing movements with the magnifying power required to introduce the necessary details, but I trust I have succeeded in giving a tolerably accurate idea of their appearance in these outline drawings. In a larva during the tenth day after fecundation (fig. 14), the most important changes are the increase of the arms e' , e''' , and the formation of rudiments of another pair of arms, e'' ; the vibratile epaulettes, v'' , as Müller has called the peculiar accumulation of vibratile cilia situated between the base of the adjoining arms e' , e''' , make their appearance at this stage. It is easy to follow them from their origin, when they are simply a thickening of the vibratile chord v'' , figs. 14, 15, until they have passed through the successive stages represented in figs. 16, 17, 19, to attain the great size observed in fig. 20, when they appear in certain positions as having no connection whatever with the vibratile chord, and to have originated independently of the main chord. Müller had not traced their development, and laid great stress on their presence in distinguishing the different species of Sea-urchin larvæ.

With the development of the arms, the intestine loses its former shape; it has now assumed the appearance of a large elliptical receiver with thin walls. The stomach is somewhat dumb-bell-shaped, and the left water-tube connects with the surrounding water, through the water-pore b , having pushed its way to the surface. The rods keep pace with the growth of the arms, fig. 15; the water-tubes have not increased in size; they are still two distinct bodies. The anal part of the outline of the larva is quite pointed; the aboral side is regularly arched, with a slight depression at the point where the water-pore opens, b , fig. 14. The opacity of the larva has increased to such an extent that it becomes impossible to define clearly the outline of the water-tubes in the stages which come between figs. 14 and 16. I am unable to state positively whether the two water-tubes are united in this and older larvæ. All I could distinctly see was the great increase in size of the water-tubes; but at the same time it becomes a puzzling matter to trace the limits of these tubes, owing to the delicate walls which bound them. Their presence can only be traced by the fine line which runs across the œsophagus from each side, and by the water-pore and the tube leading to it; b , fig. 16. In a profile view of a larva considerably older than that represented in fig. 15, the

epaulettes, v'' , fig. 16, have assumed a more independent position, forming a curve somewhat similar to the arc from which the median anal arms of the Brachiolaria are developed; the third pair of arms bulges out quite prominently, e^v , when seen in profile; the fourth pair of arms is visible, e'' ; the rod which eventually extends in the interior of it is a straight rod (r'') with a slight point in the middle, at present disconnected from the remaining part of the calcareous framework. This set of rods and the fork r''' , which extends into the arms e^v , take their origin independently from the main rod, extending from the anal part round by the mouth, from which branches are sent into the arms e' and e''' . The rod r'' ultimately combines with the main system, but the rod r''' always remains separate from the others. The position of these rods is better understood from fig. 17 when seen from the aboral side.

The stage represented in fig. 17 is particularly important, as it is at this time that we notice the first trace of what I suppose becomes the tentacular pentagon of the young Sea-urchin. On the left water-tube we notice a very prominent loop, t , which, from its resemblance to the tentacular loops of Brachiolaria and from its position on the water-tube connecting with the water-pore, I have no hesitation in considering to be the first tentacular loop formed. Compare figs. 1, 2, of Plate VII. of Müller's seventh Memoir,* where he figures a similar tentacular loop in two different stages of development; unfortunately, there is nothing in the text to explain what Müller considered it to be. The relation of this loop to the madreporic body is perfectly plain in this same larva seen from above as it is floating in the water, fig. 18, the epaulettes appearing like great flaps extending between the base of the arms e' and e'' , in continuation of the chord of cilia extending along these arms.

Figs. 17 and 18 are larvæ twenty-three days old; during the next four days no change of any importance could be perceived; the tentacular loop remained the same, the arms alone increasing in size, and a few dark pigment spots appeared in the arms. Unfortunately, at the end of these four weeks the young Sea-urchins all died. I have only once succeeded in keeping them such a long time, and that was during the coldest winter weather. In the attempts made in the spring, whenever a warm day came, it was sure to kill everything; while in the summer, though the facilities I had were infinitely greater, I never could keep these larvæ alive more than three or four days. The Sea-urchins spawn during the whole year. Successful artificial fecundations have been made in December, January, and during every month from that time till the middle of October.

* MÜLLER, J. Ueber die Gattungen der Seeigellarven. Berlin, 1855.

The remaining observations of this paper were all made from specimens caught swimming on the surface of the water; this applies to the fully-formed Sea-urchins as well as the larvæ, only the most advanced specimens (fig. 28) were found thrown up on the beach after a storm, attached to *Laminaria*. The specimens obtained in this way, the various stages of which were traced until there could be no doubt to what species they belong, connect so nearly with specimens obtained from artificial fecundation as to leave but few gaps to fill, in the larval condition, to give us all their transformations. The Sea-urchins raised from larvæ caught swimming freely about were kept in confinement until they had attained the size of some of the more advanced nomadic Sea-urchins, figs. 26, 27. This can leave no doubt to which of our two species of Echinoids these larvæ should be referred.

The next oldest larva, which is fig. 19, shows that since the last stage represented the principal changes have taken place in the oral part of the larva, fig. 19; the arms e'' , e''' especially have increased greatly in length, the outline of the anal extremity is somewhat rounded, the rod which runs along its edges is made up of short, stout pieces with strong pointed projections, and the rods of the arms are composed of three rods connected together by transverse spokes; it requires close examination to distinguish this. On the aboral side two very prominent spurs project over the stomach, somewhat below the point of junction of the rods of the arms e' , e'' , e''' . Additional tentacular loops have been formed; we can distinctly trace three on the surface of the left water-tube w' ; the outline of a part of the right water-tube (w) shows great increase in the volume of the tube. In an adult Sea-urchin *Pluteus*, fig. 20, the Sea-urchin has encroached so much on the anal extremity as to conceal the shape of the digestive cavity. The spines are so large, that we are unable to trace the position of the tentacular system; the anal opening is very conspicuous. The vibratile epaulettes, v'' , are remarkably powerful. The arms have attained nearly the same length. The vibratile chord has been twisted in such a manner as to assume the appearance of binding an anal and an oral plastron, of which e' , e'' , e''' , and e''' are respectively the arms; the mode of formation of the chord and of the arms shows that all these arms in reality belong to one plastron (see figs. 12, 13), notwithstanding the great resemblance to the two distinct plastrons of a *Brachiolaria*. Two very prominent black spots are seen in the arms e' , e'' , similar to those observed by Müller in his *Pluteus quadrimaculatus*; a few small spots are scattered over the other arms. The *Pluteus* figured here in its natural attitude does not undergo any further changes of form; it now enters a stage when the Sea-urchin goes through its greatest transformations; these unfortunately cannot be followed, owing to the opacity of the larva.

The presence of rods in the plutean forms of Ophiurans and Echinoids of course restricts considerably the play of the arms in assisting the motion of the larva. The arms cannot be bent and twisted in the graceful manner so peculiar to Brachiolaria. They are only capable of opening and shutting like the rods of an umbrella. Fig. 21, which is fig. 20 seen from above, when left in its natural attitude, shows the extent to which the arms can be spread. This does not prevent the larva from moving quite rapidly by means of a kind of gliding motion, in which the vibratile epaulettes perform an important part in propelling the Pluteus. While moving, the anal extremity is usually kept below, as in the position which has been given to all the figures in this Memoir, which is their *natural position*. Previous to the time when the anal extremity is loaded down by the presence of the Sea-urchin (figs. 1 – 19), it is quite common to see them moving in every possible direction, so that it would be difficult, from a knowledge of the earlier stages alone, to ascertain with precision what the natural attitude is; although we notice even in the early periods a very strong tendency to assume the natural position of the adult larva. The larvæ also assume during their movements the oblique position described in Brachiolaria; this seems characteristic of all the Echinoderm larvæ I have had occasion to examine, whether Ophiuran, Holothurian, Echinoid, or Asterian. A natural profile view of an adult larva (fig. 22) cannot be made with great accuracy, and the outline here given is added simply to show the position of the arms; rotating as they do almost continually on their vertical axis, we catch only passing glimpses of the exact profile outline. The only adult larva figured in profile by Müller is on Plate V. of his seventh Memoir.

An adult Pluteus, in the condition of fig. 20, requires several weeks for the completion of the Echinus and the absorption of the plutean framework. The Echinus encroaches gradually on the anal extremity; the base of the arms, e' and e'' , is soon lost in the midst of the spines of the young Sea-urchin, which are arranged in a conical open spiral wreath surrounding the mouth, fig. 23. While this encroachment of the anal extremity is going on, the œsophagus has contracted to such an extent that the base of the oral arms, e''' , e'''' , is brought directly in contact with the anal vibratile chord. During the process of resorption the arms have lost their mobility; they appear like helpless rods, stretching at every conceivable angle from the Pluteus, which has lost entirely its former symmetrical appearance, fig. 23.

The young Echinus after the Resorption of the Pluteus.

The figures given by Müller on Plate III. of his first Memoir* represent several

* MÜLLER, J. Ueber die Larven und die Metamorphose der Ophiuren und Seeigel. Berlin, 1848.

Echinoid larvæ in which the young Echinus has absorbed more or less of the plutean frame. From what I have observed on several of these larvæ, the Pluteus is as completely resorbed as is the case in the Brachiolaria observed by me. Not a single part of the framework is thrown off; this process of resorption begins at the base of the arms; they are thus gradually shortened, the rods apparently melt away before our eyes, the extremity of the arms is the last to disappear, and immediately before the time when the young Echinus is freed from the plutean appendages, the extremities of all the arms are still there, as perfect as when these appendages stretched symmetrically on both sides of the longitudinal axis. From many of the figures of Müller himself it is evident that, in the larvæ he has observed, the young Echinus resorbs the whole of the framework, and does not separate from it by losing the arms, as he has stated. See Plates III., IV., V., VI. of the first, and Plate VIII. of his seventh Memoir. The larva represented in fig. 20 of this paper was kept in confinement from the 1st of October to the 20th of November before every trace of the arms had disappeared, and the young Sea-urchin had assumed the appearance of fig. 24. Fig. 24 was drawn from a specimen found floating on the surface in the middle of June. This young Sea-urchin bears a striking resemblance to a young Echinocidaris figured by Müller on Plate IV. of his seventh Memoir. The development of the separate parts is very different in the two. The number of spines is much greater in our *Toxopneustes*, and they are of an entirely different shape. Pedicellaria are likewise present in Echinocidaris; * these do not make their appearance till a much later period in our young Sea-urchins. (See fig. 28, *p.*) What is particularly characteristic of these earlier stages of the young Sea-urchins is the great size and small number of the spines. Their position is also peculiar; they are all placed on the edge of the test, which is exceedingly flat. (Compare this with *Podophora*.) Five of the tentacles are strikingly prominent, equalling in length the diameter of the shell; they are also remarkable for their great thickness, and the presence of a calcareous ring in the sucker, which is entirely wanting in young Starfishes. A similar calcareous ring is figured by Müller,

* The function of pedicellaria has long been a puzzle to naturalists. While watching a Sea-urchin which was discharging its excrements, I noticed that the pellets always moved in definite paths, down the interambulacral spaces, till they were pushed off from the test. On examining this with a magnifying-glass, I could distinctly see the innumerable pedicellaria hard at work seizing in their tiny prongs the pellets which they pushed down the interambulacral areas. If by chance a pellet found its way into the ambulacral zone and came in contact with the suckers, it was immediately seized by the ambulacral pedicellaria and thrown back into the interambulacral zone to move on in its accustomed path. The pedicellaria are more numerous in the interambulacral zone than in the ambulacral. This will explain the function of these pedicellaria, at least for Sea-urchins, as that of scavengers.

Plate IV. fig. 13, seventh Memoir, and Plate VII. fig. 2, first Memoir. The whole abactinal surface is thickly covered with dark crimson pigment-cells. The younger spines resemble those of the young Starfish (see fig. 16, Proc. Am. Ac., l. c.), while the more advanced spines are not fan-shaped, but slightly pointed, reminding us of spines of *Cidaris*. On turning this Sea-urchin on its actinal side, as in fig. 26, we find near the base of each of the five large tentacles four others, which are not as advanced, and are incapable of expanding beyond the edge of the test.

Additional spines are formed on the abactinal side of the test of older specimens (fig. 25), so that they cover the whole of that surface, and are no longer limited to its edge, as in fig. 24; the large spines become more pointed, the tentacles grow slender, and they can all expand beyond the edge of the test. The odd tentacle expands and contracts to a remarkable extent, sometimes as much as three times the radius. The four other tentacles are somewhat more stout, and not capable of such extensive expansion and contraction; the pair of tentacles placed nearest the mouth is the stoutest. The position of the tentacles is best seen from the actinal side (fig. 26). The whole actinal surface is covered with a plating of limestone cells, which leave but a small circular opening, the mouth, in which the points of the teeth project. This actinal system is circular; there are no notches for the passage of the gills, as in adult *Echini*; the ambulacral tentacles are placed one above the other. The long spines move in every direction, as they are already provided with the peculiar ball-and-socket joint of *Echinoids*. On removing the spines of one of these young Sea-urchins, the great size of the tubercles (*n*, *n'*, fig. 27) and the large circular actinal system give them an aspect totally different from what we are accustomed to associate with the genus *Toxopneustes*. The teeth (*k*, fig. 27) fill but a small part of the actinal system; they are five narrow triangular wedges, extending from the centre to the edge of the shell, covered partially by the network of limestone plates. (See fig. 27.) The test thus denuded of its spines resembles in all the general features that of a *Cidaris*. With the exception of the formation of the abactinal system, which is not yet developed, the striking features of the young Sea-urchin — such as the circular actinal system, its large size, the great prominence of the tubercles, the position of the pores one above the other — are all characters belonging to a different family from that to which the adult Sea-urchin belongs. The little Sea-urchin does not long retain these anomalous features; with every day of increasing age the changes which it undergoes bring it closer and closer to the condition of the adult. In a young Sea-urchin of a diameter of one fifteenth of an inch (fig. 28) the spines have lost almost entirely their embryonic character, the tentacles are much more numerous, and pedicellaria have made

their appearance; in the interambulacral space they are more thickly scattered than in the ambulacral, where there are merely three or four. The abactinal system consists of a single large plate covering the opening of the anus (*a*) which leads out on one side of it. The additional spines and plates which have been formed are all developed from the abactinal region. The new plates are added in a spiral manner round the anal plate by additions to the limestone mass, pushing further away from the abactinal pole the first formed plates. The outline of the new plates is at first indicated on the lower edge, which becomes somewhat undulated; then the transverse divisions are made, and a spine is formed on the plate soon after that. There are no spines on the last formed plates; the spines when they first appear have the same fan-shaped character as the earliest formed spines of the abactinal surface. (Figs. 24, 25.) This shape they lose soon, and pass at once into spines resembling the older ones in every respect except size.

The mode of formation of the new plates was discovered by Professor Agassiz as early as 1834, when he gave a short account of it in the *Edinburgh Philosophical Journal*. The spiral arrangement of the plates is still very plainly visible in adult specimens. Although the Sea-urchins are circular, we have in their mode of growth something which reminds us of the earlier embryonic stages of the Starfish. I have not been able to trace all the various stages of growth of the young Sea-urchin, how it passes from fig. 28 to the condition when the pores, instead of being arranged in single rows one above the other, are placed in arcs on both sides of a median ambulacral row covered with spines. We may, however, form a tolerably accurate idea of the changes which must be gone through by examining the abactinal part of the ambulacral area of an adult Sea-urchin. The mode of formation of the ovarian and ocular plates remains still to be traced. The oldest of the young Sea-urchins (fig. 28) has advanced sufficiently to enable us to see that the subsequent changes which are required to make it agree with its adult condition are by no means as great as the changes which the young Sea-urchin has undergone up to the present time. It has reached a condition which assures us that we deal with a young *Toxopneustes*, and nothing else. The pigment spots, so marked in the younger stages, are smaller and scattered more uniformly, the muscular band around the mouth is well developed, the plate covering the actinal area has separated from the edge of the test, and is moved by the muscular membrane which covers the actinal system. There are no notches as yet in the actinal part of the test. The teeth have not changed their form from that found in earlier stages (fig. 27); there are from seven to eight tubercles in each vertical row of the ambulacral and interambulacral zones. I was unable to distinguish

among the many tentacles the original odd tentacle which was so prominent in the younger stages. Neither have I succeeded in determining the position of the eye in any of the stages of these young Sea-urchins, owing to the early presence of the spines and of the large pigment-cells, which prevent us from obtaining a favorable view of the odd terminal tentacle in the young forms; neither have I been able to satisfy myself whether this odd terminal tentacle retains its original position during the whole life of the Sea-urchin, as is the case in the Starfish. I can likewise say nothing concerning the development of additional ambulacral tentacles.

The figures of young Sea-urchins which Müller has given belong unfortunately nearly all to different suborders from our Toxopneustes, so that we cannot make the comparison with our young Sea-urchins as close as we might wish; and besides this, the figures of Müller are not drawn in such a way as to discriminate between the parts which belong to the ambulacral and interambulacral spaces. This is particularly evident in his figures from the mouth side, where we frequently find tentacles in such numbers as must make the development of the different ambulacra unequal. The same is the case with the spines. Any one who will take the trouble to compare the figures of young Sea-urchins of Plates IV. and VII. of his first Memoir, Plate VII. fourth Memoir, and Plate IV. seventh Memoir, with the figures given here (figs. 24-28), will see that, although they agree in their general characters, yet it is impossible to place the different spines or tentacles in such positions that they will be divided into ambulacral and interambulacral regions, which is easily done with the figures I have given. We must remember, however, that most of Müller's figures are Clypeastroids and Spatangoids, which may make it difficult, if not impossible, to divide the young Sea-urchin into ambulacral and interambulacral areas, where we have nothing like regular vertical rows to guide us, as in our Toxopneustes. One great difference, however, will strike us at once; it is, that what Müller has called anus I have in my figures called mouth. The view he has taken is probably due to the fact that the young Sea-urchins from which he made his drawings were compressed. Having followed the mouth in the different stages which have been represented here, I think there can be but little doubt that Müller was mistaken. Compare fig. 26 of this paper with his fig. 3, Plate VII. first Memoir, and we cannot fail to come to the conclusion that it is the mouth which is turned towards us in both cases. If Müller's statement were correct, we should have the anomaly in young Sea-urchins of finding all the tentacles between the spines and the anus on the abactinal side of the test, while on the actinal area we should have nothing but a closed membrane. This is so contrary to the plan of development of Echinoderms, whether Echinoids, Starfishes, or Ophiurans,

from the observations of Müller himself, that I give the accompanying explanation, which seems to bring the figures of Müller in accordance with what I have observed. The appearance of the teeth, in Müller's figures, on what seems the abactinal side, is due to compression also. The spines of the young Sea-urchins observed by Müller have a very uniform appearance; they are nearly all hexagonal prisms in their earliest stages. The same is the case with our young Sea-urchins, though they lose their embryonic character at an earlier period than is the case in any species observed by Müller.

Embryological classification of Echinoids.

From a careful examination of the different stages through which our young Sea-urchin passes during its development, and after comparing these stages to forms resembling them which are now found living in our seas, we obtain valuable hints as to the relative standing of the different families of some Echinoids. We can extend this somewhat to other orders by availing ourselves of the additional observations of Müller, and of a few facts concerning the development of Clypeastroids noticed by Professor Agassiz, which will be given here. Professor Agassiz's observations were made upon young specimens of *Mellita testudinata* Kl., which is so common along the whole of our Southern coast, from Beaufort, N. C., to Texas; upon the young stages of *Echinarachnius parma* Gray, which are found in great quantities in the stomach of our Cods; and on the young of an Encope, probably *Encope Valenciennesii* Ag. The observations on *Mellita* I had occasion to repeat on an allied species, *Mellita longifissa* Mich., which is exceedingly numerous on the beaches in the neighborhood of Acapulco, Mexico.

The smallest specimens of *Mellita* observed, measuring about one seventh of an inch in diameter, are nearly circular; they have but a single lunule placed in the posterior interambulacral space; this is no larger than the prick of a needle. With advancing age, measuring one fifth of an inch, its outline has not varied much; the lunule has grown larger. When it has attained a diameter of one third of an inch, the outline becomes slightly indented at the place where the two posterior ambulacral lunules will eventually be developed. As the posterior interambulacral lunule is not homologous to the others, but is simply an opening for the anus, we have in the first stages described a condition which reminds us at once of *Echinarachnius*. It next loses its circular outline, becoming somewhat eccentrically elliptical, as in *Dendraster*; while after the formation of the two posterior lunules it has all the aspect of a *Lobophora*. As it increases in size two other indentations are formed, the indication of the position of the two anterior ambulacral lunules. These lunules remain open for a considerable period of the growth of the urchin; we cannot fail to recognize in this state of the

young *Mellita* a strong resemblance to *Encope Michelini* Ag. and *Echinoglycus* (*Lobophora Stokesii* Ag.). The anterior ambulacral lunule is last formed. The posterior lunules then close, and had we not the anterior notches we should have an *Amphiope*. The last step, which is the closing of the three anterior lunules, gives to the young *Mellita* the general aspect of the adult; it has then attained a diameter of three quarters of an inch. In the young of *Encope* the same succession of changes is observed; at first they are circular, with simple notches in place of the posterior lunules; the anterior lunules are then formed, the posterior ones close, and, last of all, the anterior ones. In the early stages it is a *Lobophora*, then an *Echinodiscus* (*Lobophora bifora* Ag.).

In the young of *Echinarachnius* the changes of form are equally important; small specimens measuring not more than one fourteenth of an inch are very elliptical in outline, the longer axis being twice as great as the shorter; the test is quite convex, resembling strikingly *Echinocyamus* and *Fibularia*; the anus is placed on the abactinal side, and not on the edge of the test, as in the adult. This shape the young soon loses to attain a more circular outline, becoming flattened, while the anus is pushed nearer the edge. In specimens in which the longer axis measured one fifth of an inch, the test is quite flat, and the anus is placed on the edge of the disk. The outline is still different from that of the adult, the longer axis being the anterior axis in these young specimens, while in the adult it is the axis at right angles to the odd ambulacrum which is the longest.

From these data important results have been drawn for the classification of Echinoids.* All Echinoids pass, in their early stages, through a condition which recalls to us the first Echinoids which made their appearance in geological ages. We should, then, on embryological grounds, place true Echini lowest, then the Clypeastroids, next the Echinolamps, and finally the Spatangoids. The true Echini are an embryological suborder; the Clypeastroids recall to us, in their young stages only, this lowest suborder. The Echinolamps have lost the teeth which characterize the first suborders, and they show a tendency to develop an upper and a lower side, a front and a behind, which is carried to its extreme among Echinoids in the Spatangoids, the highest suborder, the young of which cannot be distinguished from those of the lower suborders at the time when they are provided with few stout spines. There are not a sufficient number of living representatives of Spatangoids and Echinolamps of which we know the development to go into more detail with respect to the standing of minor groups. In Clypeastroids what has preceded seems to show that we must place *Fibularia* and

* L. AGASSIZ. Essay on Classification.

Echinocyamus lowest; then the rounded Clypeasters, Clypeaster and Rhaphydoclypus, in which we have the floor connected by but few supports; then forms such as Laganum; then the circular Scutellæ, such as Arachnoides, in which the anus is supramarginal; then Echinarachnius, Dendraster, Scaphechinus; then the genera Lobophora, Echinodiscus, Echinoglycus, Encope, Rotula, and Mellita.

Adapting in a similar way the observations of the different stages of our young Echinus given in this Memoir to the true Echinoids, we should for similar reasons place lowest the family of Cidaridæ; next, the Diadematidæ; then that peculiarly embryonic family, the Echinometradæ, in which the unwinding of the pentagons leaves the Sea-urchin with oblique axes; then Sea-urchins with few larger spines, such as the Echinocidaridæ and Heliocidaridæ. In all these families, with the exception of the Heliocidaridæ and Echinometradæ, the ambulacral system is particularly simple. We next have those Sea-urchins with a more complicated ambulacral system, in which the tubercles become numerous and are not arranged in such regular vertical rows as in the true Echinidæ, Toxopneustes, and the like; then the Hipponoidæ, and the like, in which the development of the ambulacral system reaches its greatest complication, in which the spines are exceedingly fine, and in many genera (such as Salmacis and Mespilia) resemble more what we find in the Clypeastroids; passing gradually through forms such as Boletia, Tripneustes, Hipponoë, Salmacis, Mespilia, to take their greatest degree of complication, both in the ambulacral and interambulacral regions, in Holopneustes.

The correspondence between the embryological development and the order of succession of Echinoids in geological times is so striking, that it may not be out of place to show some of the principal points of agreement.* The number of fossil Echinoids known is so great, that, when we have as large a number of embryonic forms for each species to compare with them as are here given for a couple of species, we shall not fail to draw most important conclusions for our knowledge of the classification of these animals.

The earliest Echinoids,† which make their appearance with the Trias, are without exception Sea-urchins, belonging to families which have eminently embryonic charac-

* See AGASSIZ, L. Catalogue Raisonné . . . des Echinodermes . . . An. des Sc. Nat., 1846 – 47.

† I omit intentionally the presence of such forms as Palæchinus in the Silurian, Eocidaris in the Devonian, and the many Archæocidaris and Melonites of the Carboniferous, until a comparative study of these forms with the younger stages of Comatula has been made. I am convinced from what I know of the embryology of Echinoderms, that they are only synthetic and prophetic Crinoids, and have therefore nothing to do with our present subject.

ters. The Cidaridæ make their appearance first, and the other genera, of which a few representatives are found, belong to a family closely allied to the Cidaridæ, the Hemicidaridæ, a prophetic and synthetic family combining features of the Cidaridæ, which have preceded them, and of the Pseudo-Diadematidæ, which are to follow them. We have not a single Clypeastroid, Echinolamp, or Spatangoid. During the Lias the Clypeastroids make their appearance, but the type which represents the suborder, the genus Collyrites, is not a Clypeastroid, as we understand them in the present epoch. It is a type which is the forerunner of the true Clypeastroids, and which apes the characters of the Spatangoids. The Echinoids of the Lias have not the strong, embryonic character which belonged to the Trias; we find such genera as Hemipedinæ, Diademopsis, and the like, which remind us forcibly of the Diadematidæ of our present time. In the lower stages of the Jurassic period the Echinoids are of still more varied genera, — such as Holoctypus and Pygaster, — being forms which recall to us the embryonic stages of our Clypeastroids. The Echinolamps are likewise introduced with Pygurus and Echinobrissus; while it is only in the lowest Cretaceous deposits that the first Spatangoids appear as Holaster and Toxaster. If we compare the appearance of the Clypeastroids in geological ages with the embryonic stages of which I have given a short account, we shall find that the first true Clypeastroids (Clypeastroids such as we know them in our own time) are such forms as Scutellina and Lenita, in the Eocene; it is only in the Myocene that the genus Clypeaster appears and takes its greatest development, accompanied with a large number of true Scutellæ; and it is not till the Pliocene that genera resembling Amphiope, Encope, and finally Mellita, make their appearance, showing a closeness of agreement between the order of development and the geological succession carried out to the fullest possible extent.

OPHIURANS.

To the extensive investigations of Müller about the embryology of Ophiurans and Holothurians I have but little to add, and I consider myself very fortunate to have been able to increase our knowledge of two of the orders of Echinoderms after what has been done by him.

Ophiopholis bellis Lym.

Two Ophiurans are quite common at Nahant; one, *Amphiura squamata* Sars; the other, *Ophiopholis bellis* Lym. The latter, unfortunately, does not lay eggs from which the plutean stage is developed, as the young Ophiurans are never nomadic. The eggs are laid in bunches, from which, according to the observations of Professor Agassiz, made as far back as 1849, the young *Ophiopholis* is developed, very much

after the manner of *Asteracanthion Mülleri* of Sars, without passing through the plutean stage. So many points of investigation have arisen since those observations were made that they must necessarily be very incomplete without a renewed comparative study of the whole subject. I here copy from the drawings of Professor Agassiz two stages of the young *Ophiopholis* which will enable us to compare the two modes of development, and show us as clearly for *Ophiurans* as I have shown for *Asteracanthion* in the fifth volume of Professor Agassiz's Contributions, that these two modes of development are but longer or shorter ways of arriving at the same point. Fig. 29 is one of the more advanced young of *Ophiopholis* seen from the abactinal side. At this stage it shows prominently the arrangement of the abactinal plates and the position of the arm-joints. As in young *Asteracanthion*, we have a central plate, and five radial and five interradial plates. No hooks or granules are as yet developed; only two of the tentacles have reached any great development, and project beyond the edge of the arms. A careful examination of the young *Ophiura* in this stage would enable us to determine the exact place where new arm-joints are added. There seems some doubt, from the observations of Müller* and of Lütken,† as to whether the new joints are formed at the base of the arms or at the extremity. From what I have observed in Starfishes, it is evident that the new parts of the actinal and abactinal portion of the arms are not added at the same place. The new suckers in the Starfishes are formed nearest to the odd terminal ocular tentacle, while the new spines of the abactinal side of the arm are formed at the base of the arm. (See Vol. V. of the Contributions of Professor Agassiz, where a full account of the increase of the arms of the young Starfish will be found.) Something similar may occur in *Ophiuridæ*, and would account for the difference of opinion entertained by Müller at different times as to where the new arm-joints were added. In fig. 30 we have the actinal side of a young *Ophiopholis* somewhat less advanced than fig. 29; there are as yet no arm-joints, and the whole outline is pentagonal; two of the tentacles alone make their way through the actinal limestone floor.

Amphiura squamata Sars.

The Pluteus of which a figure is here given (fig. 31) is probably the larva of *Amphiura squamata*. I have found these larvæ only three times during two summers, — once in June, once in July, and then the young *Ophiuran* (figs. 32 and 33) during the first week of October. It probably requires as long a time as this for the development of the Echinoderm, as I have kept the larvæ which were caught in June

* MÜLLER, J. Memoir I., 1848, and Memoir V., 1852.

† LÜTKEN, C. F. Additamenta ad Historiam Ophiuridarum. Kjobenhavn, 1858.

and July for weeks without noticing any striking changes. These Ophiuran larvæ resemble very closely the Pluteus of *Ophiothrix fragilis* and the *Pluteus bimaculatus* of Trieste, figured by Müller in his Memoir on the Ophiuran Larvæ of the Adriatic.* Fig. 31 resembles more Müller's fig. 1, Plate VII. of the Memoir just quoted, than any other. The order of appearance of the arms of this Pluteus agrees with his observations on the younger stages of the Pluteus of *Ophiothrix fragilis*. (Memoir V., Plate VI. figs. 8–12.) This has been traced in a specimen considerably younger than the one figured here, resembling Müller's figure of *Pluteus bimaculatus* (Plate I. fig. 1, Memoir V.), with the exception of the different degree of development of the arms C and D of that figure. In this younger Pluteus, the arms corresponding to e' of fig. 31 were the longest; next the arms e^v , then e''' , the arms e'' scarcely projecting from the curve joining e''' and e' . The arms e' in the adult larvæ are twice as long as the others (fig. 31), while the other arms, e'' , e''' , e^v , are all nearly equally developed. With the exception of this difference in the proportion of the arms, the younger larvæ did not differ in the essential parts from the one which is figured here. The most complete histories which Müller has given us of the development of any Echinoderms are those of *Pluteus bimaculatus* and of *Ophiothrix fragilis*. He gives us not only the complete history of the changes of the larva, but follows the young Ophiuran after it has absorbed its calcareous framework. Here, again, the figures of Müller seem to contradict his text; he says the framework is dropped, but his figures show that, on the contrary, nothing is lost, that every part of the Pluteus is absorbed by the Echinoderm. See Müller's figures of Memoir V., Plates IV., V., VI., VII., VIII. Fig. 5, Plate VII. agrees exactly with the stage represented by me in figs. 32, 33; the long arms e' are cut off for want of room; every other arm can be traced, with its extremity perfect, disappearing gradually into the substance of the Ophiuran. This Pluteus is quite transparent, and did it occur in sufficient numbers it would be as favorable a species to follow the development of the Echinoderm as the Brachiolaria of our Starfishes.

The greater similarity of the Ophiuran larva to Echinoids than to Starfishes is something very peculiar. The same thing we find again repeated for two of the other orders; the larvæ of Holothurians and of Starfishes resemble each other to a remarkable extent, in the character of the arms, the absence of rods, and the aspect of the water-tubes. In Ophiurans and Echinoids this resemblance is still closer. The arms are supported by rods in both, the water-tubes are small, and the general outline of

* MÜLLER, J. Ueber die Ophiurenlarven des Adriatischen Meeres. Fünfte Abhandlung. Berlin, 1852.

the plutean forms is so similar that they might easily, on first examination, be mistaken for larvæ of the same orders.

All I wish to show from the figure of this Pluteus (fig. 31) is that in Ophiurans, as well as in Echinoids and in Starfishes, the Echinoderm is developed on the water-tubes, — one (the left) developing the actinal, the other (the right) developing the abactinal region, — that the tentacular pentagon is open in the larval condition, and is only closed by a process of unwinding, some time after the actinal and abactinal surfaces have been formed, though this closing takes place in Ophiurans and Echinoids while the Echinoderm still retains parts of the framework. In Starfishes, on the contrary, the closing of the pentagons takes place after the resorption of the Brachiolaria. From the position of the water-tubes it is self-evident that the loops of the pentagon of tentacles (fig. 31, *t*) are not in one plane; they connect with the water-tube *b*, and we find all the essential features of the tentacular water-tube (*w'*) of the Brachiolaria. (See Proc. Am. Acad., l. c., fig. 12.) The tube *w* is not connected with the tentacular water-tube *w'*. It would be interesting to observe whether such a connection takes place, also the mode of formation of the first limestone particles on the water-tube *w*, as this would facilitate the study of the development of the same parts in Echinoids where the opacity of the larva prevents accurate observations. Müller has, in nearly all his figures of the Ophiuran plutean forms, represented the water-tubes as made up of two distinct parts, having no connection. This probably arose from the strong contraction of the water-tubes in certain parts. I have noticed in the larvæ which I observed a marked tendency in the anal portion of the water-tubes to contract, and thus apparently to divide off from the remainder of the water-tubes; this was, however, but temporary, and the moment afterwards the water-tubes had assumed again their fully expanded shape, as in fig. 31, *w*, *w'*. The young Ophiurans (figs. 32, 33) are remarkable for the total absence of the plates of the disk; they are not even indicated by the presence of Y-shaped limestone rods. The only calcareous deposits we have (*y*, *y'*, fig. 32) are evidently parts of the first arm-joints, the dorsal (*y*, fig. 32) and side arm-shields (*y'*, fig. 32) of that joint, which consist at present of but a few rods, indicating their future position. The arms *e'* are the last to be resorbed; in the stage of fig. 32 they retain their full length; the other arms, *e''*, *e'''*, *e''''*, are in a very contracted condition, as they have been almost entirely resorbed by the young Ophiuran, leaving nothing but the extremities; the rods of two of the arms are not entirely resorbed (fig. 32).

This young Ophiuran, seen from the lower side, fig. 33, shows that the tentacular pentagon has entirely closed. The ambulacral system is similar to the tentacles of

the young Starfish, and must have been formed in a similar way from the original simple loops of fig. 31. (See Proc. Am. Acad., fig. 15.) Additional tentacles are therefore formed at the base of the odd loop t' , probably in the same manner as in *Asteracanthion*. The mouth is not limited by the formation of the actinal floor; this, as well as the abactinal area, is in the present stage almost entirely made up of the remaining portions of the *Pluteus*, which have not been resorbed, and through which the parts of the young *Ophiuran* are seen.

The number of young *Ophiuridæ* observed is not sufficient to enable us to make much use of their earlier condition for a classification. The figures of the young given by Müller, and the few species of which Lütken has studied some of the earlier forms, together with the observations of Kröyer,* are all we have. The figures of young *Astrophyton eucnemis* M. T., given by Lütken in his *Additamenta ad Historiam Ophiuridarum*, throw some light on the classification of *Ophiuridæ*. Having had the opportunity to examine very young specimens of *Astrophyton Agassizii* Stimp., collected at Eastport, Me. by Mr. Verrill for the Museum at Cambridge, I was enabled to repeat his observations, and find the same remarkable differences between young and adult which had already been pointed out by Lütken. A young *Astrophyton* would seem at first glance to belong rather to *Asteronyx* or *Asteroporpa* than to *Astrophyton*. The disk is circular; there are no ribs; the arms have but a single fork. The ribs on the disk make their appearance when each arm has divided three times; that is, when there are twenty terminal points. Up to that period the rounded plates of the disk were quite prominent, somewhat resembling in their arrangement those of the disk of *Ophiopholis*. This is sufficient to show that the *Astrophytidæ* stand highest among *Ophiurans*; that *Ophiurans* with smooth arms, as *Ophiura*, are lowest; next come such genera as *Ophioglypha* and *Amphiura*; *Ophiopholis* next; while *Ophiocoma*, *Ophiothrix*, and the like, in which the spines take their greatest development, stand highest among *Ophiuridæ* proper.

The stages represented in figs. 32 and 33 are somewhat different from any given by Müller; the nearest conditions are those of fig. 2, Plate VII. and fig. 4, Plate IV. fifth Memoir, in which the outline of the young *Ophiuran* is far less well defined, but in which the abactinal plates, as well as the arm plates, are further advanced; the condition of the tentacles is nearly identical. In its general outline fig. 33 differs but little from fig. 30, where the abactinal and actinal floors are more advanced, showing otherwise no differences which would lead us to suppose that the mode of develop-

* KRÖYER. Nat. Tidsskrift, III., 1840.

ment of these two forms was apparently so contrary. Let us take the *Pluteus* at the time of the appearance of the young Ophiuran, and deprive it of its arms, we should soon find our *Pluteus* in a condition in which the nomadic and sedentary mode of development could not be distinguished; showing us that for Ophiurans, as well as for Starfishes, these two modes of growth, at first so different, reach, early in the development of the young, stages which are identical.*

HOLOTHURIANS.

Cuvieria Fabricii Dub. et Kor.

In Holothurians the two modes of development seem to combine in a very remarkable manner. The larva has short arms only in the early stages; it remains nomadic after they have disappeared, when it would be very difficult to tell by which of the two modes the young Holothurians have been developed. See Müller's figures, in which the *Auricularia* approaches the "Walzenförmige" form, fourth Memoir, Plate I. From the young Holothurians which I have myself observed I am not able to say anything concerning the water-tubes, and must therefore make a comparison of the Memoirs of Müller with what has been suggested here. Although we have a *Synapta* and a *Chirodota* (*Caudina arenata* Stimp.) which are very common here, all my attempts at artificial fecundation, or at finding their plutean stages with the other Echinoderm larvæ, have completely failed. The only Holothurian of which I have seen the young is *Cuvieria*, which is tolerably abundant in deep water off Nahant, and of which the young, in the more advanced stages only, however, are found from June to October. The study of the development of an *Auricularia* with reference to the part the water-tubes play in this would be particularly interesting.

Holothurians are the only Echinoderms studied by Müller in which he distinctly says that the young Holothurian resorbs the whole of the pupa, as he calls the envelope of the Holothurian, and which lose nothing during the development. On account of this resorption, he considers the plan of the Holothurian development to be something special. I trust I have made it sufficiently clear that resorption takes

* The fact that *Ophiopholis* lays its eggs in bunches seems to lessen the difference between the Echinoderms which lay eggs and those which are viviparous, or retain the eggs in bunches in a sort of pouch at the base of the anus, as in fig. 34, which figure shows the manner in which a small *Asteracanthion*, allied to *A. Mülleri* Sars, retains its eggs till they have reached a very advanced stage of development. This figure is borrowed from drawings made for Professor Agassiz in 1848. In the Ophiurans, also, the young of some species are retained in the body of the parent till they reach a very advanced condition. Quatrefages has observed this. Professor Agassiz and Dr. Simpson have also noticed it in a species from Charleston, and Mr. Theodore Lyman observed it on the coast of France. See also Schultze and Krohn in Müll. Arch. for 1852 and 1857.

place in Starfishes, Echinoids, and Ophiurans, as well as Holothurians, and thus the distinction drawn by Müller falls to the ground. The young of *Cuvieria* figured here resemble the figures of Müller on Plate IV. third Memoir,* and Plate VII. fourth Memoir.† The young Holothurians (figs. 35 – 38) can without doubt be referred to *Cuvieria* on account of their color; they are of a brilliant vermilion. This unfortunately renders them so opaque that we cannot trace the position of the different organs without strong compression. In the youngest *Cuvieria* observed (fig. 35), the pupa (*l*) is very large; the Holothurian has not resorbed it to any extent; the tentacles (*g*) cannot be protruded. In a somewhat more advanced specimen (fig. 36), the Holothurian seems to have resorbed a considerable portion of the pupa (*l*); the tentacles (*g*) protrude; they are simple, do not branch, and terminate with knobs. The only tentacles present are those round the mouth. In a still more advanced stage (fig. 37), the tentacles show the first tendency to forking (*g*); other tentacles, ambulacral tentacles (*g'*), are also developed. The madreporic body stands out at the extremity of a small tentacle, *b*. That this is truly the madreporic body can easily be seen by compressing specimens of the age of fig. 36, when the madreporic body will be seen at the extremity of a tube, connecting thus the outer medium with the water-tubes in exactly the same manner as in Starfishes, Echinoids, and Ophiurans. The presence, also, of a calcareous network, is the best proof of its future function. During resorption this canal becomes liberated, but shrinks soon so as to bring the madreporic body on a level with the general outline.

On compressing a young Holothurian, about in the state of fig. 37, we shall obtain an idea of the state of development of the different parts. Fig. 38 (a Holothurian thus compressed) shows the separation of the main cavity into a kind of œsophagus, a stomach, *d*; and an intestine, *c*, with the anus, *a*. In younger specimens, when compressed, there is no anus, and the stomach is a simple sac without the peculiar bent addition of the intestine, *c*, of fig. 38. There are likewise no Y-shaped rods deposited on the surface of the body, and the ring of limestone particles at the base of the tentacles is not as fully developed as in this figure. (Fig. 38.) The madreporic body is seen more clearly in younger stages to connect with a large sac, *w'*, which is probably the remnant of one of the water-tubes, from its connection with the tube leading to *b*. Although externally (fig. 37) we see but two ambulacral tentacles, yet on compressing this specimen we should find that there were others already formed, but in such a rudimentary state that they do not as yet force their

* MÜLLER, J. Ueber die Larven und die Metamorphose der Holothurien und Asterien. Berlin, 1850.

† MÜLLER, J. Ueber die Larven und die Metamorphose der Echinodermen. Berlin, 1852.

way through the envelope, *l*. When compressed, the mode of branching of the young tentacles is clearly seen.

Incomplete as these observations are, they are of considerable value in a zoölogical point of view. It is evident that those Holothurians which want the ambulacral tentacles,* and have only a limited number of tentacles round the mouth, such as *Caudina*, *Synapta*, *Fistularia* (the *Apodes*), in which there are but very few deposits of limestone particles, stand lower than those Holothurians in which, as in *Cuvieria* and *Psolus*, some of the ambulacra are provided with suckers, forming a kind of sole, and in which the limestone particles perform an important part in covering the body. We should therefore place higher still those Holothurians in which, as in the preceding group, the tentacles round the mouth have a highly ramified character, and which have besides ambulacral suckers equally developed on the different ambulacræ. It is evident from this that several of the forms observed by Forbes,† such as *Psolinus*, etc., will prove to be only the young of *Pentacta*, since he has distinguished genera principally from the degree of development of the gills and of the ambulacral system.

GENERAL PLAN OF DEVELOPMENT.

The figures of Müller show without doubt that in Holothurians as well as Echinoids the young Echinoderm is in its earliest stages an open spiral star. An examination of the figures of Plates III. figs. 6–9, V. figs. 5–8, and Plate VI. first Memoir, and of Plates VI. fig. 14, VII. figs. 4, 6, 7, 9, and IX. figs. 3, 4, fourth Memoir, will satisfy any one that his figures cannot be made to agree with one another on any other supposition than that of an open pentagonal spiral surface which develops the actinal system of Echinoids on the surface of one water-tube, and of a similar spiral surface on the other water-tube which develops the abactinal area. In the same way Müller's figures of *Auricularia*, particularly those of Plate I. fourth Memoir, and Plate III. sixth Memoir, show that the young Holothurian also commences by having an open spiral actinal tentacular system. The figures of young *Auricularians* which are given on Plate I. fourth Memoir also show without doubt that the tube which leads to *b*, in fig. 36 of this Memoir, is the tube leading from the water-tubes to the dorsal pore, and that *b* is really the madreporic body. Müller also considers it as such in his figures, and it is certainly very remarkable that, with the admirable figures he has given of the young Ophiuran and *Auricularian*, he should not have noticed the intimate connection of the water-tubes and of the young Echinoderms. It is natural that the

* L. AGASSIZ. *Methods of Study*. 1863.

† FORBES, E. *A History of the British Starfishes*.

idea which he entertained, that we had in Echinoderms a passage from the bilateral to the radiated form, should have made such a strong impression as to prevent his noticing the radiated character of the young embryo, hidden as it is by all this external appearance of bilateral symmetry. And had it not been for the clear idea we have now of the character of the parts of radiated animals,* I doubt not that Müller's view would have gained general acceptance among investigators, and the whole framework of classification, based upon the idea that a plan pervades the different types of the animal kingdom, would have fallen to the ground, if it could have been clearly proven that in Echinoderms we had a transition from one of these plans to another.

As embryology gives us the means of distinguishing on broad principles the class of Batrachians from that of the true Reptiles, since it has been shown conclusively by Professor Agassiz that the Batrachians are an eminently embryonic class, while the Reptiles proper are a synthetic type, so the embryology of Echinoderms throws a new light on the character of the orders which compose that class. Particularly important is this knowledge when applied to those early forms which have been considered by some geologists as Starfishes, Echinoids, or Ophiurans, thus placing the first appearance of these orders far back in geological times. A comparison of these types with the embryonic forms of our Starfishes, Sea-urchins, and Ophiurans, will show us plainly that they have nothing in common with them. The few features which have misled investigators, and have prevented their recognition as true Crinoids, are either synthetic or prophetic characters. Crinoids are an eminently synthetic and prophetic type. From the time of the earliest appearance of Crinoids the characters which they combined foreshadowed the advent of the true Starfishes, the Ophiurans, and the Echinoids. The synthetic characters were so prominently developed that many of them are readily mistaken for Starfishes or Sea-urchins, for the same reasons which have made it so difficult to recognize as true Reptiles those synthetic forms in which Fish or Batrachian features concealed the true Reptilian character, until we had obtained a reliable guide in the distinctions pointed out by embryology. If these views are correct, the Crinoids are the only Echinoderms which are found in the Palæozoic period, and it is not until the Secondary that the other orders appear.

The Starfishes as an order are characterized by the absence of prophetic features. They are rather a parembryonic order; that is, certain features which are character-

* L. AGASSIZ. Contributions to the Nat. Hist. of the U. S., Vols. III., IV.

istic of the embryos of Echinoderms are carried to a great prominence in the different families. These are, to give a few examples, the great development of the marginal plates of the arms, the character of the spines on the abactinal area, and the presence of pointed tentacles in the adult Starfishes. Ophiurans, on the contrary, are a peculiarly embryonic order. They never develop interambulacral plates, which, as we shall see in *Asteracanthion*,* develop quite late in the life of the young Starfish. What is very remarkable in all the young Echinoderms is their Crinoidal character. A stem added to a very young Starfish, Ophiuran, or Echinoid recalls to us many of the forms with which we are familiar in the palæontological history of our earth, and I have no doubt that a comparative study of the innumerable Crinoids known, and of the living and fossil Echinoids, Starfishes, and Ophiurans, will bring out many more points of interest than have been here alluded to, and give us a correct idea, not only of the nature of the orders, but also of the families which compose them. I have here pointed out a few of the characters which distinguish the different orders of Echinoderms; I shall endeavor to adopt the same method, to show how far what we know of the embryology of Echinoderms will assist us in forming a true conception of the classification of Radiates, reserving closer comparisons between the development of Acalephs and Echinoderms for another occasion, when I shall treat more fully than I have room for here of the development of the Ctenophoræ, which gives us the connecting link between the Polypoidal and Echinodermal mode of development. The division of Cœlenterata, proposed by Leuckart in contradistinction to Echinoderms, does not correspond to any natural distinction we can draw between the mode of development of Echinoderms on the one side, and that of Polyps and Acalephs on the other. The mode of development of Polyps differs more from that of the higher Acalephs — the Ctenophoræ, for instance — than that of the Ctenophoræ differs from the Echinoderms. But what is a fatal objection to the division proposed by Leuckart is the appearance at the earliest stages of development of definite numbers of spheromeres, whether we deal with a Polyp, an Acaleph, or an Echinoderm; and these spheromeres are not simply analogous parts, as the tentacles of the embryos of some Annelids and the arms of the plutean state of Echinoderms, but are strictly homologous, showing plainly that the same plan underlies the mode of development of these three classes, though it is carried out in such different ways in Polyps, Acalephs, and Echinoderms, and that the separation of the great type of Radiates into two branches, as proposed by Leuckart, is an artificial division which has no true foundation in nature.

* See Vol. V. of *Contrib. Nat. Hist. U. S.*, by L. Agassiz.

EXPLANATION OF THE FIGURES.

WITH the exception of figs. 29, 30, and 34, which were copied from drawings made by Mr. Tappan, under the direction of Professor Agassiz, the figures were drawn on wood by myself from the drawings I made at the time of this investigation.

TOXOPNEUSTES DROBACHIENSIS AG.

FIGS. 1-28.

The specimens from figs. 1-18 inclusive were all obtained from artificial fecundation; figs. 19-27 were caught with the dip-net; fig. 28 was thrown up on the beach after a storm.

EXPLANATION OF LETTERING.

<i>a</i> , anus.	<i>r''</i> , rod of arm <i>e''</i> .
<i>b</i> , madreporic body.	<i>r'''</i> , independent rod above œsophagus.
<i>c</i> , alimentary canal (intestine).	<i>r^{iv}</i> , anal point of junction of rods in the Ophiuran Pluteus.
<i>d</i> , digestive cavity (stomach).	<i>s</i> , actinal region.
<i>e'</i> , <i>e''</i> , <i>e'''</i> , <i>e^{iv}</i> , arms of the plutean form.	<i>s'</i> , spots of arms <i>e'</i> , <i>e''</i> of the Pluteus of Echinus.
<i>f</i> , brachiolar arms?	<i>s''</i> , interambulacral spines of Echinus.
<i>g</i> , tentacles round actinostome in Cuvieria.	<i>s'''</i> , younger spines of Echinus.
<i>g'</i> , ambulacral tentacles of Cuvieria.	<i>t</i> , tentacles.
<i>k</i> , teeth of young Echinus.	<i>t'</i> , odd terminal tentacle.
<i>l</i> , body of larva of Cuvieria (pupa of Müller).	<i>v</i> , anal part of vibratile chord.
<i>m</i> , mouth.	<i>v'</i> , oral portion of vibratile chord.
<i>n</i> , interambulacral tubercles of Echinus.	<i>v''</i> , vibratile epaulettes.
<i>n'</i> , ambulacral tubercles.	<i>w</i> , water-tube.
<i>o</i> , œsophagus.	<i>w'</i> , water-tube leading to madreporic body.
<i>p</i> , pedicellaria.	<i>y</i> , terminal arm-plate of Ophiuran.
<i>r</i> , abactinal region.	<i>y'</i> , side arm-plates of Ophiuran.
<i>r'</i> , main rod, formed first in the Echinus Pluteus.	In fig. 31 <i>v</i> should be <i>v'</i> , and <i>vice versa</i> .

For the earlier stages compare figs. 1-5 of Proc. Am. Acad., from which the earlier stages of the Echinus Pluteus do not differ greatly.

Fig. 1. Profile view of an Echinus Pluteus eighty-eight hours after artificial fecundation.

Fig. 2. The same as fig. 1, seen from above.

Fig. 3. Profile view of a plutean form somewhat more advanced than in fig. 1; the digestive cavity, *d*, is bent very considerably towards the actinal side.

Fig. 4. View from above of a Pluteus in which the digestive cavity, *d*, is somewhat differentiated by con-

strictions; the pouch, *o*, formed at the blind extremity, has sent off two diverticula, *w*, *w'*; the first appearance of the water-tubes. End of fourth day.

Fig. 5. Profile view of an embryo somewhat more advanced than fig. 4, at the beginning of the fifth day; the intestine, *c*, stomach, *d*, and œsophagus, *o*, are well separated; the water-tube, *w'*, also stands out prominently from the extremity of the œsophagus, *o*; the anal part of vibratile chord, *v*, bulges out considerably.

Fig. 6 is a view, from the mouth-side, of the stage the embryo has attained at the end of the fifth day. The water-tubes, *w*, *w'*, have different degrees of development, and are less closely connected with the œsophagus; the rods have sent out processes at points where the new arms are to be developed, at *v*.

Fig. 7 is a view of fig. 6 from the anal extremity, to show the changes of form since fig. 2, and the position of the vibratile chord.

Fig. 8 is a profile view of fig. 6; the mouth, *m*, is not yet opened.

Fig. 9. A profile view of an embryo taken at the beginning of the seventh day; the mouth, *m*, is opened; the water-tube, *w'*, reaches nearly the dorsal surface. The currents which previously to this stage had carried the food through the only opening, *a*, as far as *o*, and then were reversed to eject the digested matter, now come in through the mouth, *m*, pass through the œsophagus, rotate about in the stomach, *d*, and pass out through the first-formed opening, the anus *a*, which is hereafter used only to eject the food.

Fig. 10. represents a *Pluteus* at the beginning of the eighth day, seen in such a manner as to show the whole of the vibratile chord, when looking on the side where the mouth and anus open.

Fig. 11 is a profile view of an embryo slightly more advanced than the one represented in fig. 10.

Fig. 12. The same as fig. 11, seen from the mouth side.

Fig. 13. Somewhat more advanced than fig. 12, seen so as to show the changes the vibratile chord has undergone since the stage represented in fig. 10.

Fig. 14. An embryo during the tenth day, seen in profile; shows the position of the arms *e'''* and *e'v*.

Fig. 15. The same as fig. 14, seen from the mouth side; the arms, *e'*, have been greatly developed; the differentiation of the intestine, *c*, the stomach, *d*, and œsophagus, *o*, is quite complete. First appearance of the vibratile epaulettes, *v''*. The water-tubes have not united; they have not greatly increased in size.

Fig. 16. Profile view during the twenty-third day; the arm, *e''*, has made its appearance, and is already quite prominent; a still greater development of the vibratile epaulettes is perceived.

Fig. 17. The same as fig. 16, seen from above, to show the relation of the different rods to each other, as well as the first appearance of the tentacular loop, *t*.

Fig. 18. View of fig. 17, corresponding to the less advanced stages of figs. 10 and 13, showing the connection of the different parts of the vibratile chord.

Fig. 19. A much more advanced stage than fig. 17, seen from above; found swimming freely on the surface of the water. The rods extending into the arms are made up of three sets of rods united by short transverse bars; additional tentacular loops have been formed. The water-tubes have greatly increased in size, and appear to have united.

Fig. 20. An adult *Pluteus* of *Toxopneustes drobachiensis*, in which the young Sea-urchin has already en-

Fig. 1.

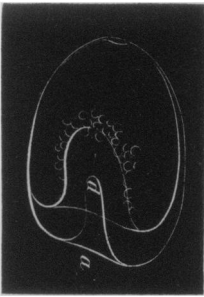


Fig. 2.

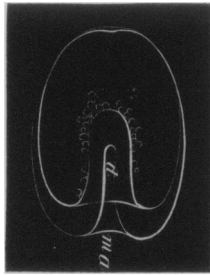


Fig. 3.

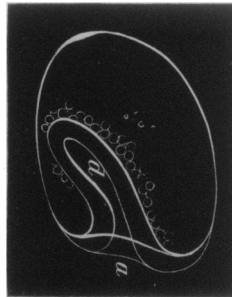


Fig. 4.

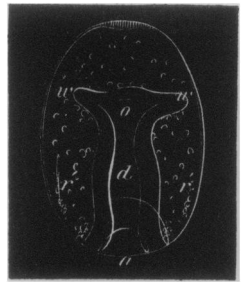


Fig. 5.

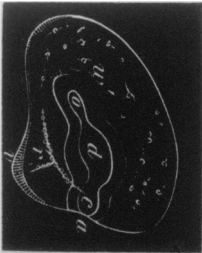


Fig. 6.

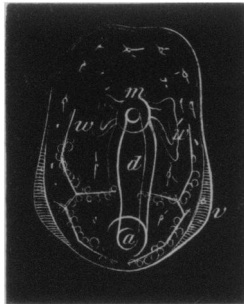


Fig. 8.

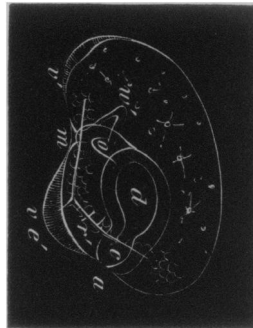


Fig. 9.



Fig. 7.

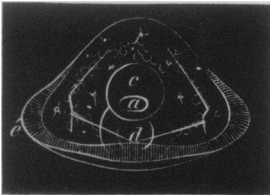


Fig. 11.

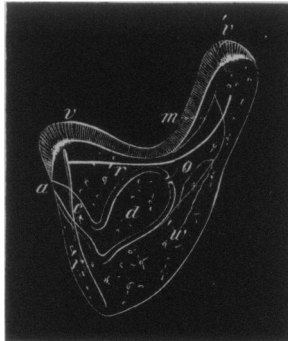


Fig. 12.

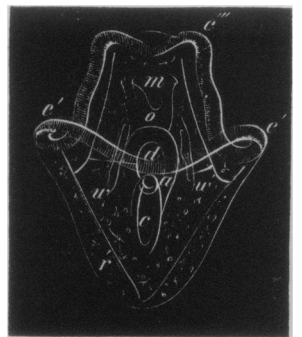


Fig. 10.

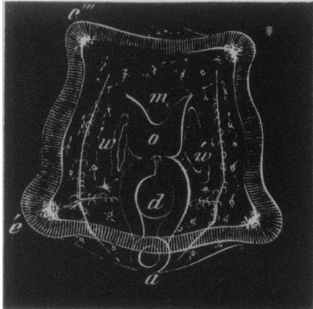


Fig. 14.

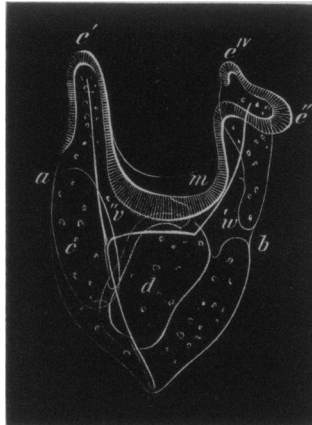


Fig. 15.

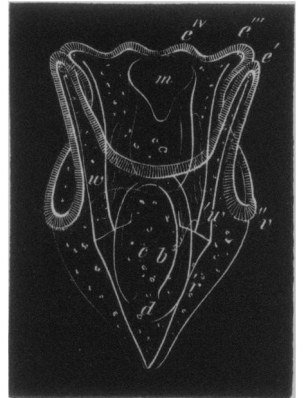


Fig. 13.

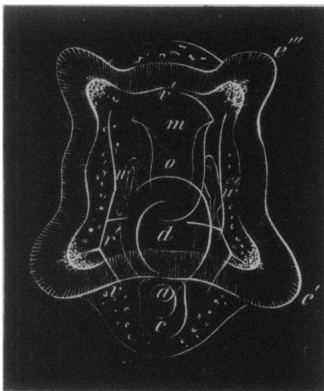


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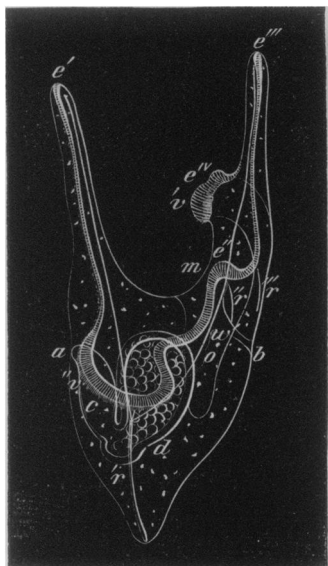


Fig. 17.

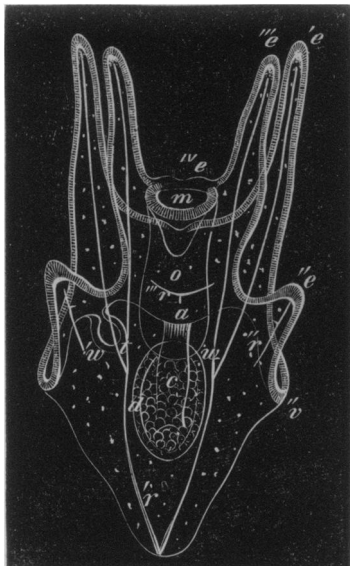


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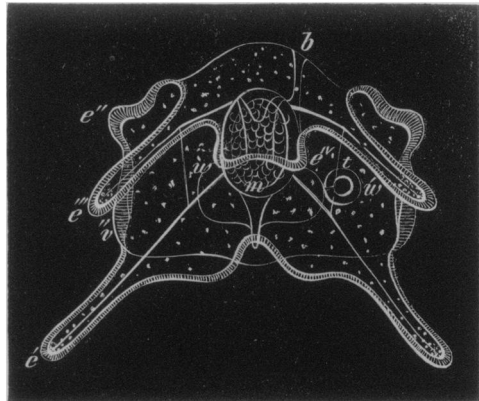


Fig. 19.

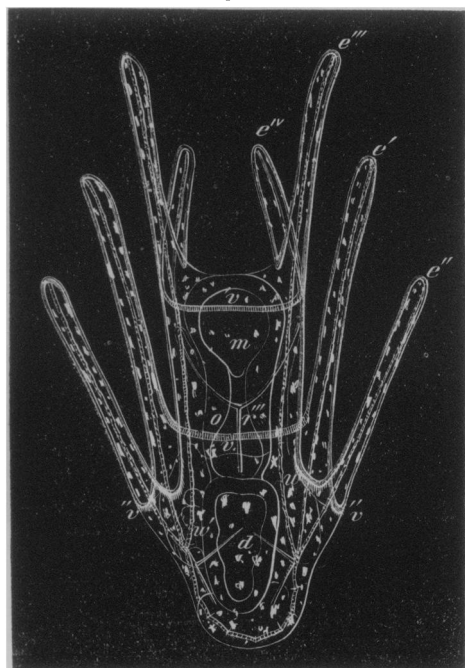


Fig. 20.

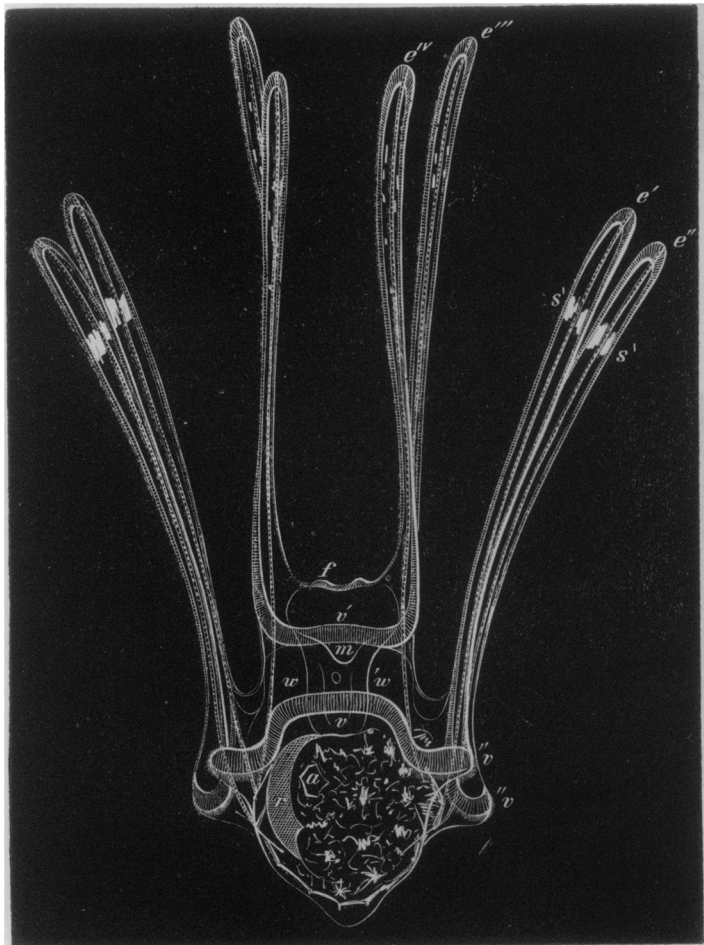


Fig. 23.

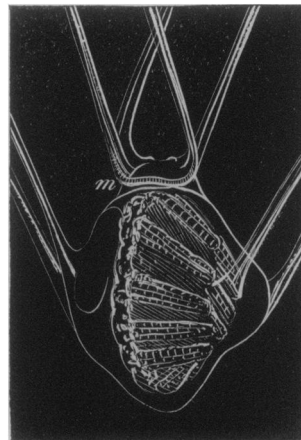


Fig. 22.

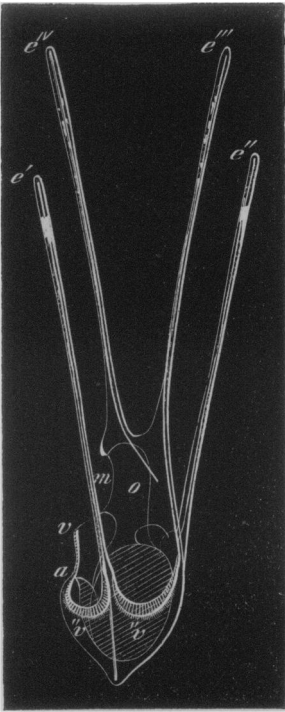


Fig. 21.

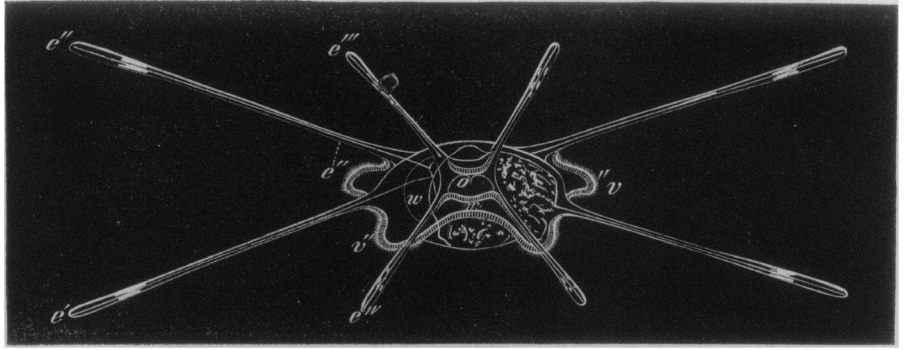


Fig. 34.

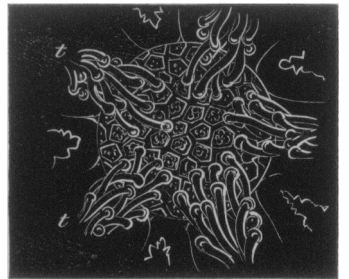


Fig. 28.

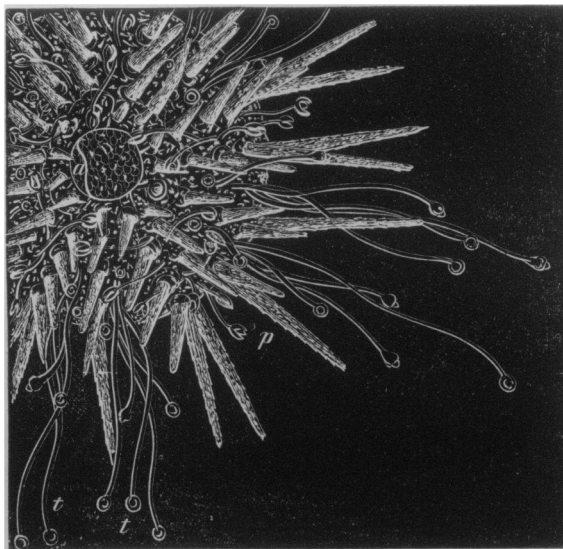


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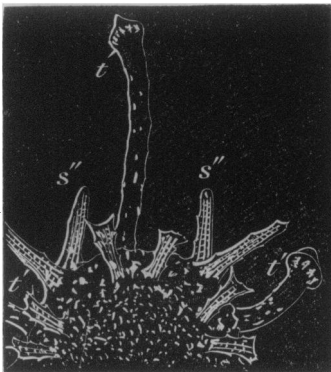


Fig. 27.

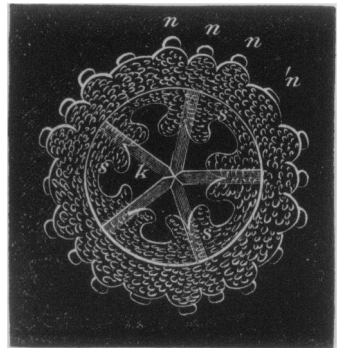


Fig. 26.

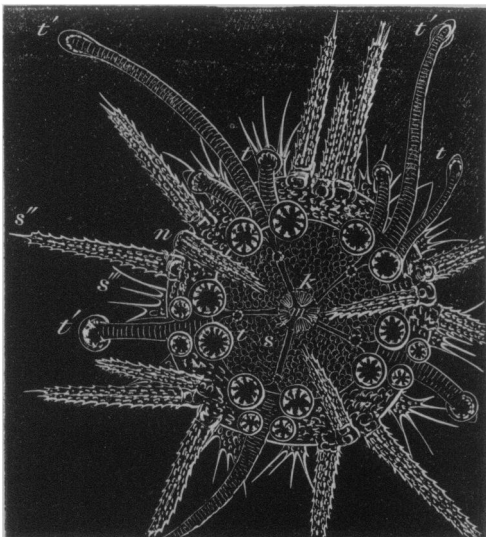


Fig. 25.

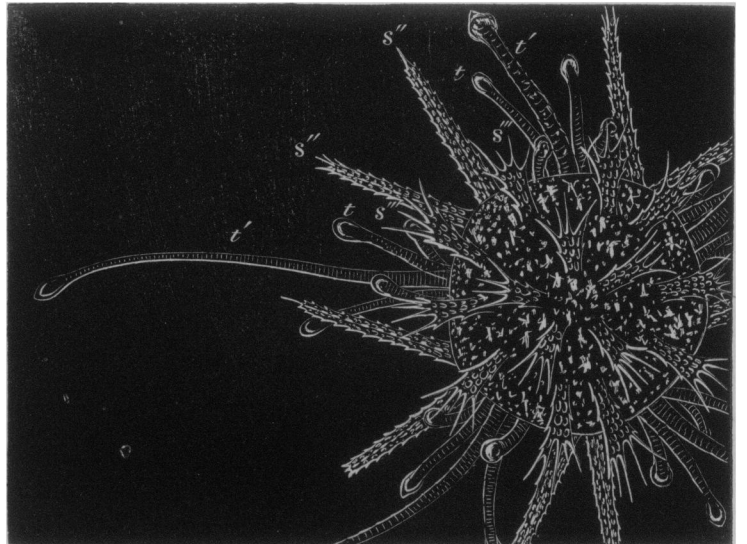


Fig. 32.

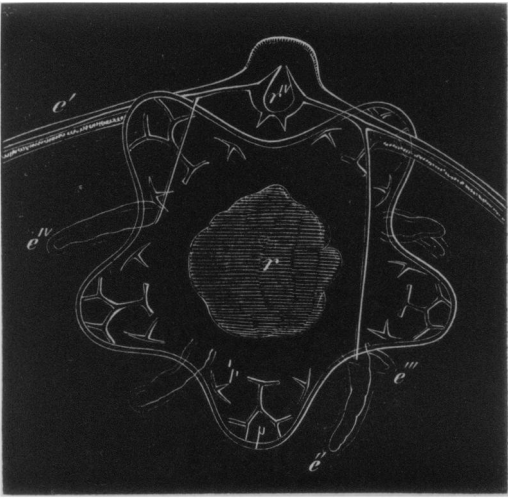


Fig. 29.

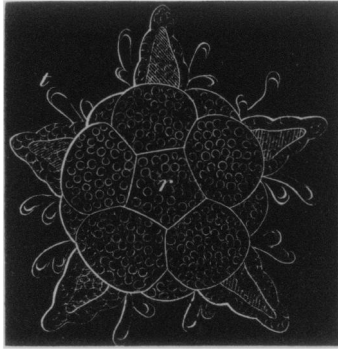


Fig. 30.

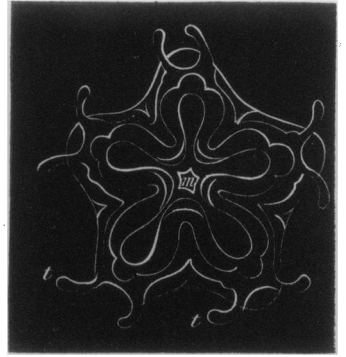


Fig. 35.

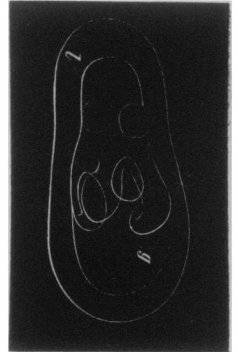


Fig. 37.

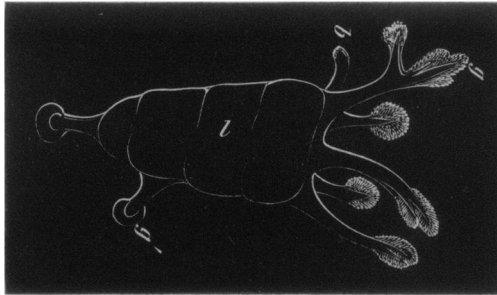


Fig. 33.

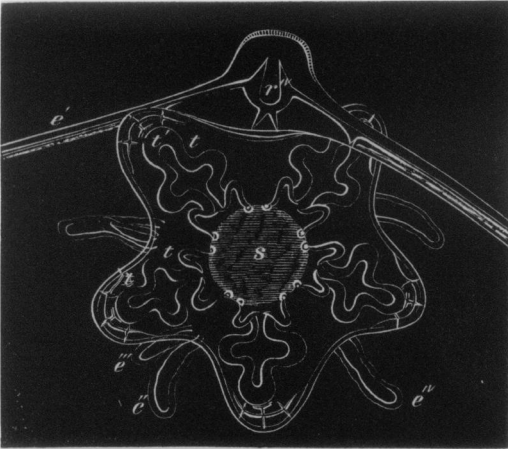


Fig. 38.

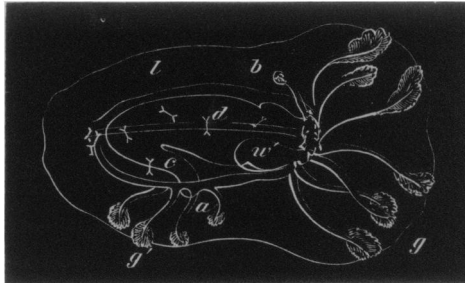


Fig. 36.

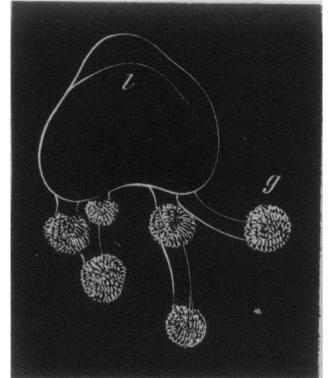
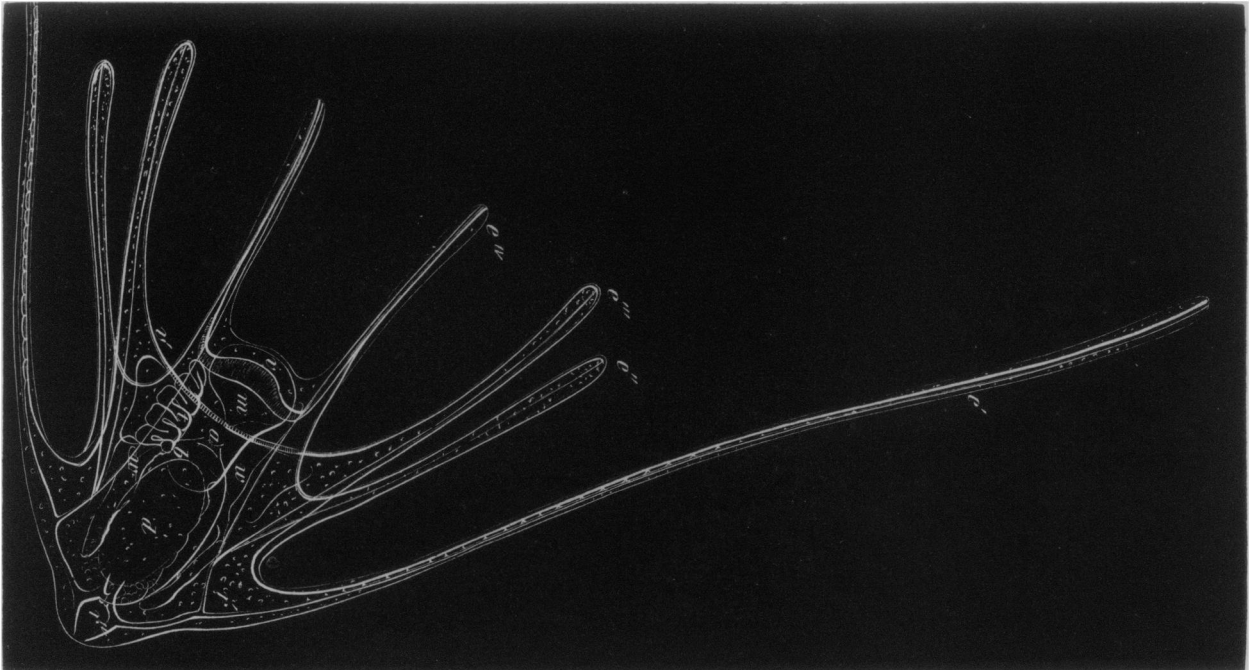


Fig. 31.



A. A. del.

croached somewhat on the anal extremity. The spines are quite prominent; the vibratile epaulettes have acquired a very large size; two very prominent spots, s, s' , in the arms, e, e'' ; f is perhaps something homologous to the brachiolarian arms of Brachiolaria.

Fig. 21. View of fig. 20, corresponding to figs. 10, 13, and 18.

Fig. 22. Profile view of fig. 20.

Fig. 23. The young Echinus has materially encroached on the Pluteus, and resorption has been carried on to such an extent that there is very little left of the Pluteus except the arms, which have lost their mobility.

Fig. 24. A young Echinus immediately after the resorption of the Pluteus, seen from the abactinal side.

Fig. 25. Young Sea-urchin somewhat more advanced than that of fig. 24, seen from the abactinal side. The opening of the anus (a , fig. 28) cannot be traced in these younger specimens, though it is very apparent in somewhat more advanced ones.

Fig. 26. The same as fig. 25, seen from the actinal side; the tentacles have become more slender; the spines more numerous than in younger stages. The actinal membrane is well developed.

Fig. 27. The same as figs. 25 and 26, stripped of its spines, seen from the actinal side.

Fig. 28 is a young Toxopneustes measuring one fifteenth of an inch in diameter, including the length of the spines, in which pedicellaria have developed, and the spines have assumed the general appearance of those of the adult.

OPHIOPHOLIS BELLIS LYMAN.

FIGS. 29, 30.

Fig. 29. Abactinal view of a young Ophiopholis, to show the arrangement of the plates of the disk.

Fig. 30. A somewhat younger Ophiopholis than fig. 29, seen from the actinal side.

AMPHIURA SQUAMATA Sars.

FIGS. 31-33.

Fig. 31. An adult Pluteus of Amphiura, in which the water-tubes are plainly seen. The figure is taken on the side of the madreporic body; one of the long arms is cut off. In this figure v' is the anal, and v the oral vibratile chord.

Fig. 32. The arms of the Pluteus are almost entirely resorbed, except the two long arms, e' , which are still intact, as in fig. 31; they are here cut off for want of space. The Ophiuran is seen from the abactinal side, to show the arrangement of the arm-plates, y, y' .

Fig. 33. The same as fig. 32, seen from the actinal side. The mouth is still very large; the tentacles, t, t' , mere loops.

ASTERACANTHION FLACCIDA Ag.

Fig. 34. Mode of carrying the embryos in *Asteracanthion flaccida*.

CUVIERIA FABRICII DÜB. ET KOR.

FIGS. 35-38.

- Fig. 35. Youngest Cuvieria observed, in which the tentacles of the mouth do not yet protrude beyond the general outline of the pupa.
- Fig. 36. A much more advanced Cuvieria than fig. 35; the tentacles, *g*, are very prominent.
- Fig. 37. A still more advanced Cuvieria, in which the position of the madreporic body, *b*, can be seen. Ambulacral tentacles, *g'*, have also been formed.
- Fig. 38. A young Cuvieria nearly in the state of fig. 37, compressed to show the relation of the different parts to each other.